A SURVEY OF THE HURON RIVER VALLEY.

I. THE ECOLOGY OF A GLACIAL LAKE.

HOWARD S. REED.

(WITH FOUR FIGURES)

I. INTRODUCTION.

IN the vicinity of Ann Arbor, Mich., there are a number of glacial lakes and ponds which at no very distant day must disappear if the processes now in operation continue. At present they exhibit conditions of such interest that it has seemed very desirable to preserve as complete a record as possible of their extent, physical characters, and biological relations as they exist today. The work here reported was carried on at the largest of the so-called "Sister lakes" west of Ann Arbor.[1] It was undertaken at the suggestion of Professor V. M. Spalding, of the University of Michigan, under whose direction the botanical survey of which it forms a part is now in progress. It has been the purpose of the writer to give an exact representation of existing facts and conditions, and to study in a somewhat quantitative manner the relative value of the several ecological processes at work; necessarily some matters of theoretical interest are discussed.

The study of a glacial lake is of peculiar interest to students of ecology. The physiography of the country in which such lakes occur was entirely rejuvenated by the glacial action, and the physiographic processes taking place now are precisely those rapid developments characteristic of new land areas. Adaptations to past conditions still remain, but with them are striking and interesting adaptations to present changing conditions. The general change has been from semi-arctic and hydrophytic to temperate and mesophytic conditions. At the same time, there

[1] A preliminary report of this work was published in the Proceedings of the Michigan Academy of Science for 1901.

has been a continuous reaction of plant life upon environment; the advancing zones leave soils behind them different from those they found. Sphagnum swamps and peat bogs, into which the lakes now under consideration are changing, are the last stages in the life history of glacial lakes.

The plant life of the small glacial lakes characteristic of southern Michigan differs distinctly from most other hydrophytic societies. It is predominantly xerophil, while that of a brook or river is predominantly hydrophil in character.[2] It differs from the flora of such lakes as have been studied by MacMillan[3] and Pieters[4] in not being influenced by waves, currents, spray, etc.

II. GEOLOGICAL HISTORY.

The lake selected for study is a "kettle-hole" in the terminal moraine which formed part of the northwestern shore of ancient Lake Maumee. It is mainly fed by springs issuing from the bottom and around the shores, though a small rivulet entering from the southeast contributes some surface water during about half the year. The lake probably came into existence at the close of the second advance of the ice sheet, and at that time it was considerably larger than at present, due to the drainage from the melting ice. For some time following the formation of the lake it was apparently subject to sudden changes in size and outline due to rapid fluctuations in the water supply. There are two similar lakes within a mile to the eastward, with which it formerly may have been continuous; at present the surface of the water is five inches lower than in either of the other two lakes.

The original lake must have been from sixty to eighty feet deep in its deeper parts, and the surplus waters were discharged through an outlet to the southwest which emptied into the Huron river. The eastern shore was fifteen or twenty rods farther east than at present; while from the southeast a wide

[2] COWLES, H. C., BOT. GAZ. 31: 145. 1901.

[3] MACMILLAN, C., Minnesota Botanical Studies, 50.

[4] PIETERS, A. J., U. S. Fish Com. Bull., pp. 57–79. 1901.

cape extended into the lake, which now appears as a hill near its southeastern corner. West and southwest of this cape the water's edge was about twenty rods back of its present position, and the former western margin was approximately parallel to the present one, but four or five rods farther inland. A shallow bay extended off toward the northwest, which is still traceable by the extension of plant zones in that direction. On account of the steepness of the northern shore, the water on that side extended only a few rods beyond its present limit.

This former extension of the lake has had a marked influence upon the present plant societies. While it prevailed it necessarily drowned out all terrestrial forms; then as the water level slowly fell the aquatic and semi-aquatic species had the first chance to get a foothold and become established upon the land which was thus gradually uncovered. This was especially the case on the east, west, and southwest shores of the lake, where, on account of the gentle slope of the bottom, there was always a wide strip of shallow water in which aquatics and semi-aquatics could get a strong foothold and become established long before it was suitable for the occupation of terrestrial forms. Even today the zone of willows is destitute of any considerable number of distinctly terrestrial plants.

At a certain stage in the recent geological history of the region, as the water level fell, the large lake was divided into two, the present lake and a similar, smaller one ten rods south of it which has all but disappeared. The fate of this smaller lake throws some light on the history of the present lake, as will be shown later.

III. PRESENT CONDITIONS.

1. PHYSIOGRAPHIC RELATIONS.—As it now exists, the extreme east and west diameter of the lake is a little more than thirteen hundred feet long, the extreme north and south diameter is seven hundred feet. Between the water's edge and the higher ground which formerly constituted the shores is a swampy border varying in width from ten feet to twenty rods. The thick growth of vegetation in this border has nearly clogged the

sluggish outlet at the southwestern corner of the lake. The border swamp is interrupted on the south side of the lake by the former delta of the brook entering at that place. The delta rises several feet above the level of the surrounding shore and differs from it very markedly in vegetation (*fig. 1*).

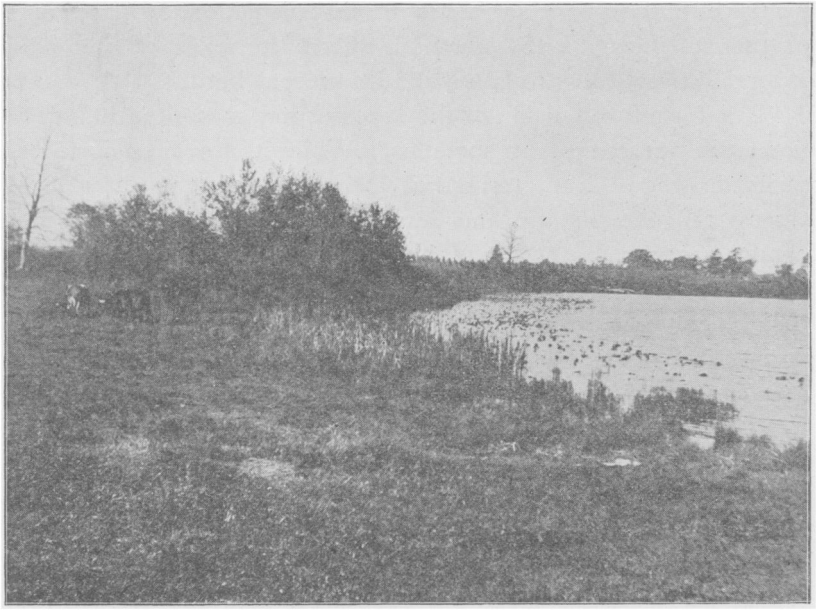

FIG. 1.—South shore of the lake, part of the former delta plain in the foreground.

The lake basin proper is surrounded by a shallow marginal rim varying from forty to seventy-five feet in width and descending from the water's edge at one side to eighteen or twenty feet below the surface at the other. This marginal rim owes its existence primarily to organic factors which are still at work modifying and extending it. The soil for several feet in depth is largely composed of organic material which presents the usual successive gradations from vegetable detritus to muck and peat. The bottom descends very rapidly from this rim to form the main central basin, which averages more than fifty feet in

depth. The soil of the central basin is almost pure loess-like clay mixed with a little fine vegetable detritus which settles from the water of the lake; this area, so far as numerous dredgings show, is entirely barren of vegetable life of any kind.

The water of the lake enters chiefly by underground channels and from springs at the bases of the gravel hills surrounding the lake. During the greater part of the year the supply is just about equal to the loss by evaporation, and except during seasons of maximum precipitation there is very little water passing into the outlet. The water dissolves and holds in solution so much organic substance from the decaying vegetation in the lake that a very perceptible taste is imparted to it. The fine detritus held in suspension together with the dissolved substance renders the water brownish, making it impossible to distinguish objects more than six feet below the surface. The opacity of the water is an important factor in determining the distribution of plants. Obviously there are no perceptible currents in so small a lake.

2. THE PLANT SOCIETIES.—The deep central portion of the lake does not, so far as could be ascertained by dredging, support any plant life; this cannot be due to the soil, for in other lakes the same soil is covered with Chara and Potamogeton, but is undoubtedly due to the feeble intensity of light at depths greater than twenty feet.

The plants at the lake are grouped in five fairly well defined concentric zones, occupying all the suitable lake bottom less than twenty feet under water, and all the land surrounding the lake which feels the influence of the presence of the water. Beginning with the innermost, they are:

(*a*) *A zone of Potamogeton*, which extends in water from eighteen feet to six feet in depth completely around the lake just shoreward of the central depression, and forms a zone averaging thirty feet in width. This zone is composed almost exclusively of *Potamogeton zosteraefolius* Schum., which grows very luxuriantly, forming a dense tangled mat. The only other plant found in this zone is *P. lucens* L.

(*b*) *A zone of Nuphar*, extending nearly around the lake, occupying the territory between the preceding zone and the water's edge. This forms a zone between thirty and seventy feet in width, whose lakeward side is about six feet below the surface of the water, while the shoreward side is limited by the

FIG. 2.—North shore of the lake; Nuphar, Carex, and Salix zones; the shrubs in the background are mostly *Populus tremuloides*.

water's edge. The most abundant and characteristic plant in this zone is *Nuphar advena* Ait. f. Its rapid growth and hardiness make it a successful competitor in the struggle among aquatic plants, and it is admirably adapted to the requirements of an advancing plant society, growing as vigorously in water six feet deep as in water six inches deep (*fig. 4*). Associated with it are *Potamogeton natans* L., *P. lucens* L., *Chara coronata* Ziz., *Dulichium spathaceum* Pers., and *Typha latifolia* L.

In places where for any reason Nuphar does not grow or grows only sparingly, *Potamogeton zosteraefolius* comes in; where Nuphar grows well Potamogeton is not found.

(*c*) *A zone of Carex and Sphagnum*, whose surface is practically at water level, extends landward from the water's edge from six to twenty-five feet. This is an exceedingly well defined zone (*fig. 2*), and lying so close to the water level it is necessarily saturated with water, and the tough mat of sedges is in many places little better than a floating morass. The soil underlying it is composed entirely of black muck and decaying vegetable matter. The most abundant plants are *Carex filiformis* L., *Sphagnum*, and *Potentilla palustris* Scop.

(*d*) *A zone of Salix and Populus*, varying from ten to forty feet wide, extends entirely around the lake and stands from three to twenty-four inches above the preceding zone. The soil of this zone is almost entirely of vegetable origin; in different parts and at different seasons it contains varying amounts of water. It never becomes mesophytic in character, and is often hydrophytic. A very few vigorous mesophytic species occur with the characteristic plants of this zone, but they usually show changes of habit to correspond to their environment. The characteristic plants of this zone are *Salix alba* L., var. *vitellina* Koch, *S. lucida* Muhl., *S. myrtilloides* L., *Populus tremuloides* Michx., and *Ulmus americana* L.

(*e*) *A zone of Gramineae and Compositae* lies just outside the last zone, and is from six to thirty inches above it. In this zone there are adaptations to past, rather than to present conditions. It is the transition zone in which mesophytic species begin to mix with hydrophytes, its landward border merges gradually into the vegetation of the surrounding country. The greatest admixture of terrestrial plants occurs on the north and southeast shores, where the struggle between plants has been most severe for some time. While it is difficult to designate distinctly characteristic plants for this zone, the following are among the most constantly recurring species: *Spiraea salicifolia* L., *Monarda fistulosa* L., *Rumex obtusifolius* L., *Eupatorium perfoliatum* L., *Salix discolor* Muhl., *Juncus canadensis* J. Gray, *Epilobium coloratum* Muhl., *Hypericum canadense* L., *Nepeta cataria* L., *Sambucus canadensis* L., *Acer rubrum* L., *Gentiana Andrewsii* Griseb., *Bidens bipinnata* L.

Careful collections were made during the entire growing season, and included practically all the species occurring at the lake. They represent forty-three families; 5 per cent. of them are natives of arctic regions; 65 per cent. are natives of North America.

3. INTERZONAL RELATIONS.—A study of the different zones and their relations to one another shows that their positions are not permanent, but that they are slowly encroaching upon the lake, and as a result are filling it with the soil they produce. Each society of plants is a more or less active soil-forming agency, and accordingly as the vegetation progressively changes the advancing zones leave a different soil from the one they found. The vigorous growth of *Potamogeton zosteraefolius* adds by its death and decay a very small amount of humus to the fine clay soil upon which it grows. Nuphar is a much more active soil-forming agent; its strong leaves and petioles projecting above the surface of the water (*fig. 2*) catch and hold most of the twigs, plants, and leaves which are blown into the margin of the lake, until they become water-soaked and sink. The débris resulting from the decay of the water lilies, added to that which they have captured, all goes to building up the bottom of the lake. On account of the limitation of Chara to the Nuphar zone, and the consequent absence of any extensive beds, it is not an active soil-forming agent by the production of marl, as it is in some of the glacial lakes of Michigan.[5]

In the intense competition among the plants of this crowded zone there is a constant tendency to move out in the direction of least resistance. Limited as it is on the landward side by less favorable conditions, the zone must make its advance, if it makes any, into deeper water, *i. e.*, into the Potamogeton zone, which it appears to do just in so far as Nuphar is able to adapt itself to the greater depth of water, or as the Potamogeton builds up the bottom. At the other side of this zone there is a tension line between the water lilies and the sedges. Whenever in any place the bottom is not more than three or four inches below the sur-

[5] DAVIS C. A., Jour. Geol. **8**: 485 and 498.

face of the water, the sedges begin to move out and occupy the territory thus prepared for them. Perhaps at first they send out a few skirmishers that occupy the top of some muskrat's mound, but generally they advance with an unbroken line and cover the soft muck with a tough quaking mat of vegetation. No advance

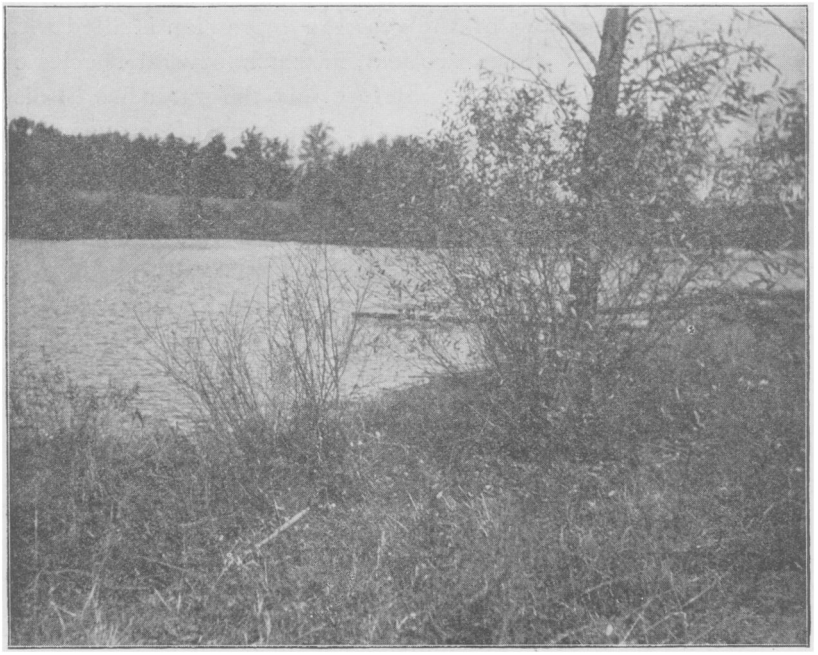

FIG. 3.—Gravelly shore at southeastern corner of the lake; absence of Nuphar and Carices results in a permanent shore-line.

of any extent is ever made without a fairly firm soil to grow upon. *Scirpus lacustris* is one of the foremost plants in the advance. As the Carex zone crowds upon the Nuphar zone, so in turn it is itself crowded upon by the Salix zone. *Salix rostrata* and *Betula pumila* are among the foremost of the plants encroaching upon the Carices. On gravelly banks and in localities where conditions are unfavorable for the growth of Nuphar, this process of filling does not occur, because the preliminary process of filling by decay cannot take place. The result is that the shore

line in such places is quite well marked and permanent (*fig. 3*).

A few rods south of the lake is the site of the "dead lake" mentioned above, a description of which may, as suggested, throw some light upon the life history of the present lake. At present the only indication of the former pond is an elliptical depression surrounded by representatives of the Gramineae and Compositae zone, but in the spring of the year the depression is filled with water to a depth of about two feet, in which several species of Polygonum grow vigorously. Before July the water has all disappeared from this basin and for the remainder of the year it is dry. In the center of the depression there is a group of sedges and ferns which is surrounded by a wide belt of willows; outside of these again is a zone of grass and terrestrial plants. The whole state of affairs suggests that this has been the site of a pond which has been steadily encroached upon by the zones of vegetation in the manner previously described, until now the pond is practically obliterated. The sedges have exterminated the water plants and now the willows have all but exterminated the sedges.

This pond, originating from the primitive lake, must have been essentially the same in character as the lake under consideration; it seems reasonable therefore to conclude that the pond represents an advanced stage yet to be realized in the life history of the lake.

IV. ECOLOGICAL FACTORS.

The plant societies afford unmistakable evidence of the influence of the glacial epochs. The flora of glacial lakes may be compared to boreal islands composed of plants forced southward by the advance of the ice sheet. The sphagnums and sedges flourish best in those conditions which best reproduce boreal environment, and so long as any plant society remains which is distinctly lacustral it will undoubtedly show traces of its boreal origin.

Agencies now at work may be considered under four groups of factors, viz.: hydrodynamic, edaphic, atmospheric, and biotic.[6]

[6] WHITFORD, H. N., BOT. GAZ. 31: 291. 1901.

(*a*) *Hydrodynamic factors*, referable to the action or presence of water. Small waves are created in the lake by high winds which would eat away the light soil composing the shores but for the fact that such shores are everywhere protected from wave action by a border of water lilies (*fig. 2*). Even in winter this action is prevented because the dead leaves remain *in situ* until the next year. The current of the brook entering from the southeast sweeps away or covers with gravel the accumulations of detritus at that point; as a result, Nuphar and its associates are not found there (*fig. 3*). Aside from this local influence hydrodynamic factors at the present time are so limited in their action that they may be disregarded.

(*b*) *Edaphic factors*, depending upon the nature of the soil. The humus in the soil formed by the decayed vegetable substances renders it very favorable for plants of the Nuphar, Typha, and Carex types. The presence of water saturated with organic matter in solution plainly influences the character of the vegetation. If Schimper's view[7] of the effect of humic acid be correct, the explanation of the xerophytic character of some of these swamp plants is that the soil is practically undrained and water with which it is saturated is rich in organic acids.

A microscopic examination of the soil from the deep basin of the lake shows that it is almost entirely composed of finely comminuted, bluish-gray clay with a very few particles of organic débris. The soil from the Nuphar zone is largely composed of fragments of epidermal tissue, moss-stems, diatom shells, bast fibers, grai s of sand, and crystals of calcium carbonate from Chara. Chemical analysis shows that nitrates and nitrites are not present in the soil, while phosphates are more abundant.

That portion of the lake bottom which is covered with soil of a calcareous or arenaceous nature does not seem favorable to the growth of the characteristic plants of the lake; the only ones which grow upon such soil are *Potamogeton zosteraefolius* and a few blue-green algae. Evidently lime-containing soils are as

[7] SCHIMPER, A. F. W., Pflanzengeographie, p. 18.

unfavorable for some other swamp plants as they are for sphagnums.[8]

The plants might be classified as to edaphic relations in the following manner: *argillaceous soil*, unattached microscopic plants, diatoms, etc.;[9] *calcareous and arenaceous soils*, Potamogeton

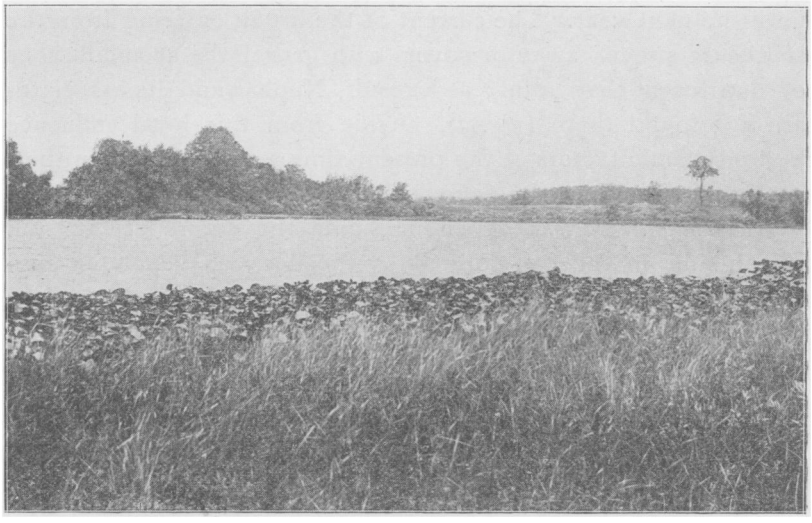

FIG. 4.—Carex and Nuphar zones, showing the massing of these plants; July 1.

zosteraefolius, Blue-green algae (rare), Scirpus lacustris, Potamogeton natans, Chara coronata, Equisetum, Panicum Crus-galli; *carbonaceous soils*, Nuphar, Typha, and Carex societies, Salices, Sphagnum, Populus.

(*c*) *Atmospheric factors.*—The most important of these is light, because, as I believe, it is this which, aside from food supply, chiefly governs the encroachment of one zone upon another. A moment's consideration will show that the plants struggling for light will have better illumination on the side of the center of the lake than on the side toward the land. Take, for example, the Carex zone (*fig. 4*). The young Carex and Sphagnum

[8] GANONG, W. F., Trans. Roy. Soc. Canada, 3: 131. 1897.

[9] Under better conditions of light, Chara and Potamogeton would doubtless occur.

plants on the landward side of the zone are overshadowed by the taller Salix and Betula plants, while on the other side there is almost nothing to diminish the supply of light. In general the plants of a zone which is successful in displacing another zone have a greater capacity for the absorption of light than those plants which they displace. One of the chief advantages of Nuphar over Potamogeton is to be found in the fact that it sends its leaves up to the surface of the water where they receive the full intensity of the light instead of the diminished amount which is able to penetrate the cloudy water to the submersed species. The lack of light caused by the cloudiness of the water seems to be the only reason for the absence of vegetation from the central deep portion of the lake.

The amount of heat which the different aquatic plants receive also varies with their distance from the surface of the water; however, they seem perfectly able to adapt themselves to these differences.

(*d*) *Biotic factors.*—Fully as important as any of the fore going factors are the conditions imposed upon plants by the presence of other plants or animals; conditions to which they must adapt themselves if they survive. The competition between different societies of plants is mainly directed toward obtaining light and food. The former has been briefly considered; there are certain biological characteristics which are favorable for obtaining the other. Perennial plants are the most successful in the interzonal struggle; they are usually adapted to xerophytic conditions by their rhizomes, waxed epidermis, and hairy surfaces. There are also special advantages in their manner of reproduction. The possession of underground rootstocks is one of the best adaptations to enable a plant to hold its own against its competitors; young plants are thus sustained by the parent plant until they are fully capable of maintaining an independent existence, and prompt occupation of a given area is easier. The advantage of the willow lies in the great number of seeds produced and the good means of disseminating them. The advantage of the sedges is in the thick mat of

rhizomes and the dense covering of long grassy leaves; the seeds are heavy and tend to fall on the territory already occupied by the parent plant.

Tension lines are the strongest where the environment is most equally favorable for each of two different societies; *e. g.*, the boundary between the Nuphar and Carex zones is the scene of a severe struggle because the conditions are almost equally suitable for both societies, but where the Nuphar zone borders immediately upon the Salix zone the tension line is weak.

The ability to compete successfully seems to depend largely upon the extent to which the plants are massed in solid ranks; such a plant society is generally able to force out other plants from the territory available for occupation. The inherent vigor and hardiness of these plant societies due to their northern origin must also be reckoned in attempting to account for the success with which they compete with other forms.

V. CONCLUSIONS.

The work as presented in the foregoing pages is the result of an attempt to study the actual operations of known ecological factors and leave a record of existing conditions in the life history of a glacial lake and its flora. Little attempt has been made to discover new factors or to modify accepted ideas of ecological principles. Most of the statements made can be verified by actual observation; some must be inferred from present conditions. If carried farther, the work should consist in verifying certain statements either by subsequent observation or by laboratory experiment. The results of my study may be summed up as follows:

1. The comparative scarcity of terrestrial plants is a result of the former exclusively hydrophytic conditions which gave aquatic species an advantage which has since been maintained by all other hydrophil species.

2. There is a striking predominance of northern species, undoubtedly the result of the glacial invasion of recent geological times, and of conditions which tend to reproduce boreal environment.

3. The strength of the tension line between zones is increased by the soil-forming activities, because the soil which each zone produces makes the lake more unfit for it and fit for the succeeding zones.

4. An interaction of organic and inorganic agencies has caused and is now causing an unmistakable advance of plants into the lake, which is gradually being filled by the soil they produce. The more important among these agencies are soil, light, and morphological advantages.

5. The struggle for existence in each zone is less successful on the landward than on the lakeward side of that zone.

6. The plants engaged in this severe struggle show a marked tendency to mass themselves in solid ranks.

BOTANICAL LABORATORY,
UNIVERSITY OF MICHIGAN.